

ON THE EXISTENCE IN HUMAN
AUDITORY PATHWAYS OF CHANNELS SELECTIVELY TUNED
TO THE MODULATION PRESENT IN
FREQUENCY-MODULATED TONES

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SUMMARY

1. The sensitivity of detecting modulation in a test tone sinusoidally frequency-modulated at a rate ϕ_{test} is diminished after exposure to a conditioning tone more deeply frequency-modulated at a rate ϕ_{cond} provided that ϕ_{cond} is not very different from ϕ_{test} , the sound amplitude being kept constant for each tone at a comfortable hearing level 40–45 dB above threshold.

2. When $\phi_{\text{cond}} = \phi_{\text{test}}$ the frequency deviation in the modulated test tone must be increased to about three times the unconditioned threshold magnitude to be detectable immediately after exposure to the conditioning tone. Detection sensitivity returns to normal in about one minute.

3. At low modulation frequencies the conditioning effects are tuned, being much diminished when ϕ_{cond} differs from ϕ_{test} by a few cycles per second.

4. Comparing monaural with contra-aural conditioning demonstrates a considerable interaural transfer of about 60–80 % of the effect, indicating that the conditioning and its selectivity are predominantly central phenomena.

5. The magnitude of the deterioration in detection sensitivity after conditioning is about $3 \times$ at modulation frequencies between about 3/sec and 30/sec. It diminishes at lower and higher modulation frequencies and is effectively absent at 100/sec modulation. The bandwidth of the effect increases from a few cycles per second at the lower end of this range, to some tens of cycles per second at the upper end.

6. For the same modulation frequency, the conditioning is relatively insensitive to the mean 'carrier' audiofrequency, f_0 . The band width in terms of carrier frequency is at least as wide as 'critical bands'. With a test signal $f_0 = 250$ Hz, $\phi_{\text{test}} = 8$ /sec, conditioning is still appreciable for a

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conditioning tone of $\phi_{\text{cond}} = 8/\text{sec}$ but centred upon $f_0 = 150$ Hz or $= 350$ Hz. Conditioning is thus not explicable in terms of coincidences between particular spectral components in the conditioning and test tones.

7. Whereas the sensitivity of detecting 8/sec amplitude modulation in a tone is conditioned by prior exposure to either amplitude- or frequency-modulated tones, in contrast the detectability of 8/sec frequency-modulated signals is conditioned only by prior exposure to frequency-modulated tones and not by amplitude-modulated conditioning tones. This underlines the special place of frequency modulation in human audition and emphasizes that the operative stimulus cannot be some aspect common to amplitude modulation and frequency modulation, like identical periodicity or coincident positioning of bands in the integrated spectra of the tones, but points to the instantaneous frequency-modulated wave form as the adequate stimulus.

8. These findings strongly suggest that the human auditory pathways contain 'channels' in their organization which determine a final response selectively tuned to particular frequency-modulations. Periodicity coding alone cannot adequately explain this effect which may well only be understood in terms of a 'place' theory of frequency selectivity.

9. This organization is well suited to subserve the recognition of frequency-modulation patterns in acoustic signals rather independently of the mean audiofrequency that carries the frequency modulation.

INTRODUCTION

It has become increasingly clear during the last few decades that the auditory pathway, particularly in its higher reaches, is at least as much organized for the detection of temporal patterns of frequency modulation in sound stimuli (Kelly & Whitfield, 1971) as it is for detecting the small tonal intervals or moderate amplitude differences between separate sinusoidal sounds of constant frequency so obsessively exploited in earlier neurophysiology and psychophysics.

This organization has become obvious not only from animal neurophysiology but also from clinical practice, e.g. in the demonstrable lack of 1:1 correspondence between the hearing loss measured by pure tone audiometry and that measured by speech audiometry. A hearing loss detected by speech audiometry is sometimes the result of a central lesion that has caused little pure tone deficit (see e.g. Schuknecht, 1970).

Denied neurophysiological access to the auditory system of man by any technique that is both useful and tolerable, one has to rely upon indirect but sometimes very powerful psychophysical tests for revealing the neural organization of a sensory pathway, as for example by adapting a parti-

cular psychophysical threshold by prior exposure of the subject to an appropriately selected conditioning stimulus. A recent example of this general technique is Blakemore & Campbell's (1969) discovery of human visual channels tuned to the spatial frequency in striped patterns of varying light intensity.

The data of animal neurophysiology already point to the importance of frequency modulation as an adequate stimulus parameter for exciting many cells in the auditory cortex (Whitfield & Evans, 1965) and in the inferior colliculus (Nelson, Erulkar & Bryan, 1966). Even at levels as low as the cochlear nuclei a special response to swept frequency can exist (Møller, 1969). These observations particularly encourage a psychophysical search for human auditory channels selectively organized to detect frequency modulation in sound stimuli.

In this paper we establish the existence and some characteristics of such channels. They prove to be tuned selectively for low frequency modulations occurring at rates between a few cycles per second and several tens of cycles per second. Their nature excludes the use of either periodicity of the modulation or spectral structure of the modulated signals as usable parameters in the stimulus, since the channels distinguish between frequency-modulated and amplitude-modulated signals which are similar in these two aspects. These channels concerned with the frequency modulation of the signal are relatively unselective for the 'carrier' audiofrequency which suffers the modulation.

A 'place' mechanism like that used for directional sensitivity in the rabbit retina (Barlow, Hill & Levick, 1964; Barlow & Levick 1965 and for movement sensitivity in the visual cortex (Hubel & Wiesel, 1959) seems likely to be needed in the auditory pathways for specially detecting frequency modulation in audible signals.

Subjects

METHODS

Most of the experiments to be described were carried out on three audiometrically experienced male subjects D.R.M. 22-24 yr, W.J.B. 36-38 yr, R.H.K. 49-51 yr, all with normal hearing for age as judged by pure tone audiometry and normal frequency discriminative ability according to the values for $\Delta f/f$ published by e.g. König (1957), Zwicker (1952) and Harris (1952). When other subjects are used they will be separately specified in the text. An indication of the observational cost of the data is given by the number at the top right of each Figure. This is the cost of the curves, the total number of observations made to determine the points shown on the Figure and it is a guide to what is necessary to attain the 95 % confidence limits indicated by the vertical bars.

Stimuli

The general arrangement of the apparatus is shown by block diagrams in Fig. 1. The final wave-form-shaping oscillator was normally a Systron-Donner type 410

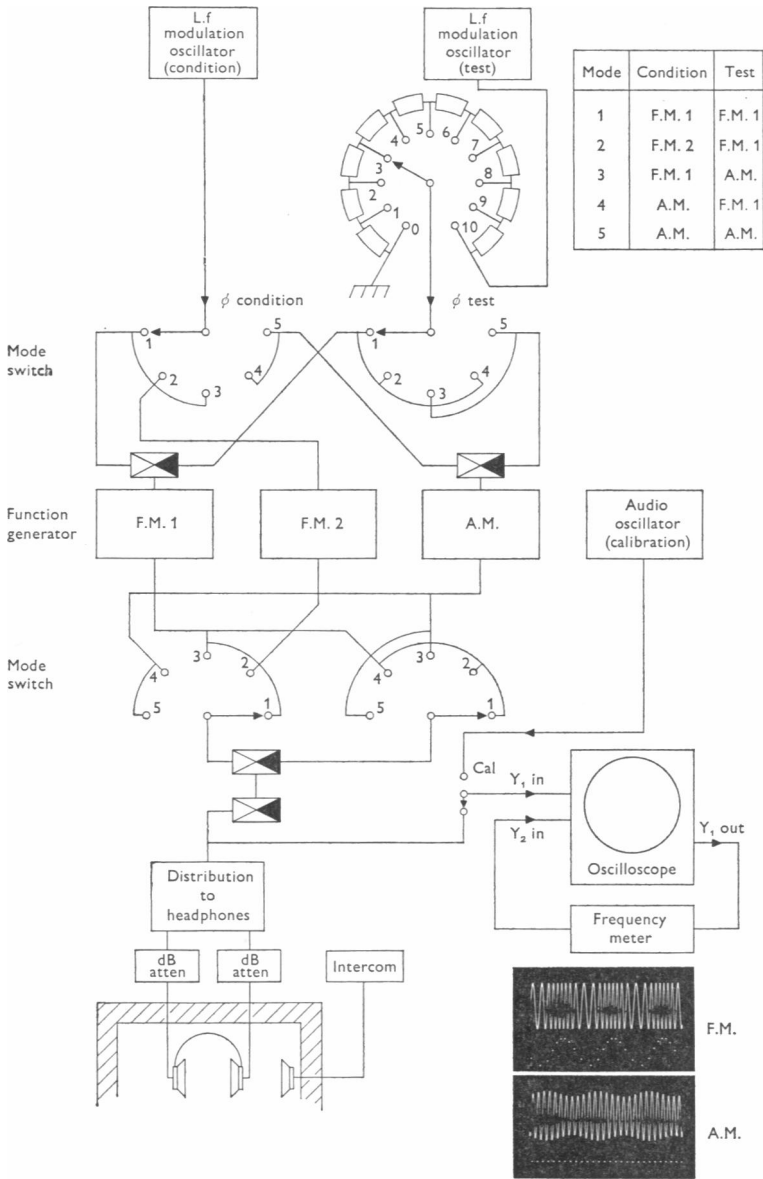


Fig. 1. Arrangement of apparatus. Inset: photographs of the simultaneous Y_1 display of sound wave form (upper beam) and Y_2 display of instantaneous frequency (lower beam), for frequency-modulated (F.M.) and amplitude-modulated (A.M.) waves.

function generator, modified by improving the layout of the power supply which as originally manufactured introduced mains frequency modulation upon the output signal. This modulation, though less than 1% and probably tolerable for most industrial use was uncomfortably near the detection threshold of man for 50 Hz frequency modulation. It has been diminished to 0.1%, more than 10 times below the human detectability threshold for 50 Hz rate of frequency modulation. The long-term frequency stability of the whole apparatus is excellent.

Sound signals were delivered from Braun AKG K60 electrodynamic earphones with circumaural earmuffs, subjects being comfortably seated (they prefer in darkness) in one of two quiet acoustically 'deadened' rooms, insulated from floor borne sound by vibration dampers, with properties like the booth described by Thornton (1967) and based on his design.

The 'instantaneous frequency' of the test and conditioning tones was continuously monitored as the DC output signal from a reciprocal pulse-interval analyser (Kay, 1965) working into the Y_2 display of a Tektronix 502A oscilloscope. Offsetting the oscilloscope zero by a DC bias applied to the other input of the Y_2 differential input amplifier allows a full scale Y_2 deflexion (10 cm) for frequency changes of one or two Hz in mean audiofrequencies of hundreds of Hz. Instantaneous frequency values and frequency deviation can be set to within 0.05 Hz.

Threshold of detection of sound was first established for each ear at the appropriate audiofrequency and then the sound amplitude was adjusted to 40 dB above threshold for binaural listening or 45 dB above threshold for monaural and contra-aural measurements (an approximately equivalent loudness). This adjustment was made separately for each subject.

Test stimuli ranging from non-modulated to supra-threshold modulations were applied in unpredictable order from tables of random numbers (Fisher & Yates, 1967). The observer was thereby prevented from introducing bias into the programme and the subjects relieved of concern that he might be doing so. The subject was required to say 'Yes' or 'No' after each presentation of a test modulation, indicating whether or not he could detect the presence of modulation. At whatever range of frequency deviation in the modulated tones being tested, test signals of zero modulation were always included to check false positives. To avoid fatigue, no separate session was allowed to last more than 10 min uninterrupted.

Treatment of the data

When a subject's answers are plotted as % 'Yes' against depth of modulation of the test tone, a sigmoid curve results. At zero test modulation a subject answers 'Yes' very infrequently, whilst at a greater modulation depth in the test tone he answers 'Yes' most of the time. We wished to establish the test tone modulation depths at which the subject would answer 'Yes' 50% and 75% of the time.

The sigmoid curves obtained experimentally can be plotted as good straight lines by transforming the % values into probits, or by plotting the % values directly on probability, rather than linear, co-ordinates. We have programmed a Wang Desk Computer to find the best-fitting straight lines of *Modulation Depth vs. Probit % Yes* for each set of observations and from these data to calculate the test modulation depths to which the subject would answer 'Yes' 50% and 75% of the time. We also calculate the slope of the probit *vs.* modulation curve, the correlation coefficient for the experimental points which determine it, and the variance and 95% confidence limits for the 50% 'Yes' and 75% 'Yes' modulation values. In Figs. 3 to 8 the 'x threshold' conditioning values are pooled 50% and 75% values determined as above, pooled for the subjects (usually three), indicated by initials in the corner of the Figure.

To determine the band width of conditioning effects we used a PDP 12 *Digital* Computer to find best-fitting Gaussian curves (as e.g. in Fig. 4 and others like it) to threshold data like the above, but determined at different modulation rates. Gaussian curves were chosen as being reasonably likely to represent the biologically laid down 'channel' and since the least squares deviation of the data points from the best fitting Gaussian curves proves to be very small we feel justified in our choice of function, without even invoking the Central Limits Theorem. The curves have the form

$$Y = 1 + Y_0 \exp - (x - \mu)^2 / 2\sigma^2,$$

where the ordinate, Y , is the detectable modulation after conditioning, in units of the unconditioned threshold; Y_0 is the maximal value of Y ; the abscissa value, X , is the modulation frequency of the conditioning tone and the value μ is that value of X at which Y is maximal (see text and Table 1). These computed best-fitting Gaussian curves were automatically plotted on paper by a COMPLIT extension to the PDP 12 (we have used best fits to both logarithmic and to linear X scaling).

(To avoid ambiguity, all modulation frequencies will be referred to by the symbol ϕ and they will be specified in c/s; all audiofrequencies will be specified by the symbol f and by Hz; and the depth of the modulation, the frequency deviation, by $\pm \Delta f$ in Hz.)

RESULTS

The sensitivity of detecting frequency-modulated sound

Before starting experiments on adaptation to frequency-modulated sound we established the unadapted sensitivity of detecting sinusoidal frequency modulation, expressed as the threshold detectable frequency deviation from the mean frequency. This was determined as a function of modulation rate in great detail for one subject and at a sufficiency of selected points to establish the characteristics of the second and third subjects' responses. These results are shown in Fig. 2 and are concerned, like the majority of results published in this present paper, with modulations centred upon a mean 'carrier' audiofrequency of 250 Hz. Below modulation frequencies of about 3/sec the threshold detectable frequency deviation is constant at around $\pm 0.15\%$, rising steadily to about $\pm 1\%$ when the modulation frequency is 25/sec or greater.

We have suggested elsewhere (Matthews, 1972) that the three straight lines of Fig. 2 define three separate regions in which the auditory pathways are organized into three different regimes of operation for detecting frequency modulation. The threshold values are in good agreement with those of Zwicker (1952) who, however, by measuring at octave intervals of modulation frequency (1, 2, 4, 8, 16, 32, etc c/s) was not able to reveal the sharp discontinuities we have found. Our points of discontinuity are closely related to and support those affirmed by Liang Chih-an & Chistovitch (1960).

In the results to be described on the adaptation of these frequency modulated thresholds by prior exposure to frequency-modulated sound we

have chosen modulation frequencies covering all three of these probably distinct regimes of operation of the human auditory system. In all measurements below, the unconditioned thresholds are determined at the appropriate modulation frequency during each experimental session for each subject; they are not assumed to remain constantly at the mean values illustrated in Fig. 2.

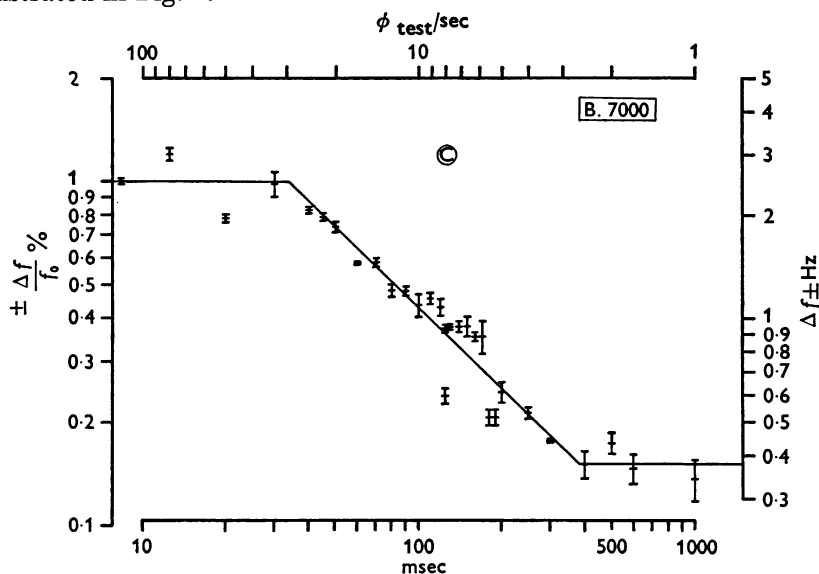


Fig. 2. The sensitivity of detecting frequency-modulated sound. Ordinate: threshold (50% detectable) modulation depth: right $\pm \Delta f$ Hz., left $\pm \Delta f/f_0$ %. Abscissa: modulation rate (above: modulation frequency ϕ_{test} /sec; below: modulation period msec). Carrier frequency, f_0 , 250 Hz. One subject W.J.B. Point C: threshold of detection at $\phi_{\text{test}} = 8/\text{sec}$ after conditioning at $\phi_{\text{cond}} = 8/\text{sec}$.

Frequency-modulation detection sensitivity after conditioning by frequency-modulated tones

(a) Time course of conditioning and adaptation

After the subject's hearing has been conditioned by listening to a tone sinusoidally frequency-modulated at a rate (ϕ_{cond}) equal to the rate of modulation (ϕ_{test}) in the testing tone and which has the same mean carrier frequency $f_0 = 250$ Hz but is frequency modulated more deeply than the test tone, by a frequency deviation $\pm \Delta f$ which is about an order of magnitude greater than the threshold detectable modulation swing, his sensitivity for detecting modulation in the test tone deteriorates to about one third his unadapted performance. As an example, for an 8/sec rate of frequency modulation the detection threshold (± 1 Hz) (see Fig. 2) deteriorates to the value marked © in Fig. 2 (± 3 Hz) after conditioning.

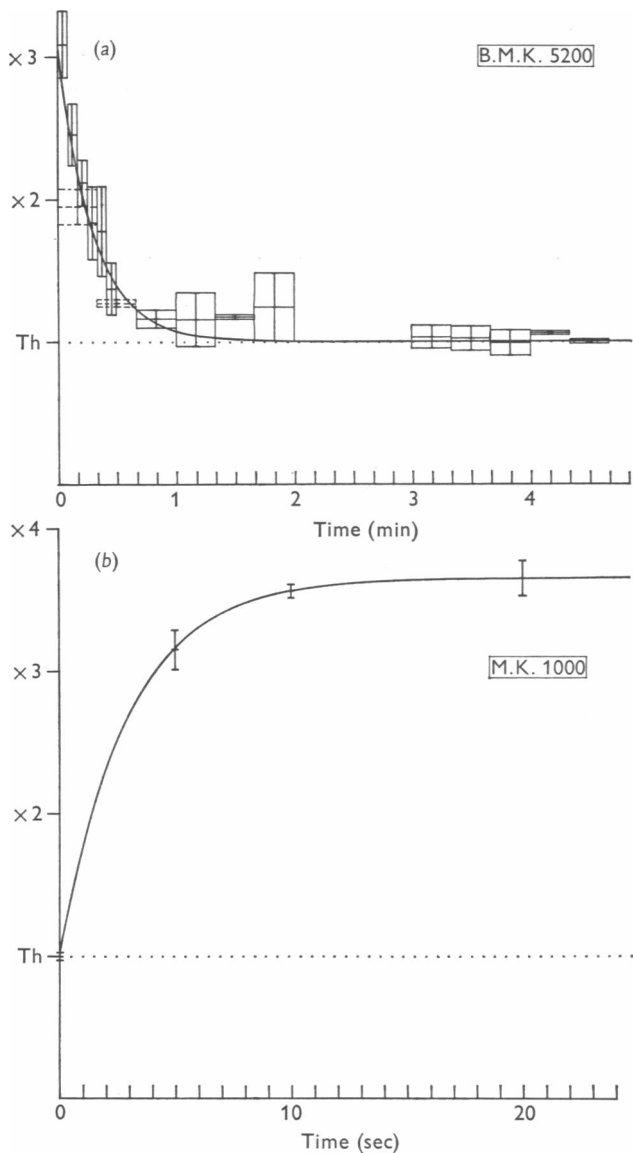


Fig. 3. (a) Deterioration in detection sensitivity after conditioning and its recovery. The recovery is well enough represented by an exponential law of time constant 19 sec. (b) Conditioning as a function of time of exposure to the conditioning tone. Time constant of the curve = 3 sec. Ordinate: deterioration in detection sensitivity (\times unconditioned threshold). Abscissa: time.

The effect is maximal immediately after the conditioning tone ceases. Thereafter the sensitivity for detecting modulation in the test tone returns to normal values within 1 min with the time course shown in Fig. 3(a). This time course is virtually identical for the three subjects studied. Its shape is well enough fitted by an exponential decay of time constant 19 sec.

Conditioning becomes near maximal after about 12 sec of exposure to the conditioning tone (Fig. 3(b)) and this time is chosen for all experiments as an acceptable compromise between the longer time for 100% conditioning with the extended observation periods which would then be imposed and the need not to weary the subjects by too long exposure, during an experimental session. This time is used for all experiments below unless otherwise specified. We also report the conditioned thresholds as those values measured within the first 3–4 sec after the conditioning tone has ceased. We shall normally report the deterioration in detection sensitivity by the ratio of the conditioned to the unconditioned threshold detectable frequency deviation (\times Thr.), rather than by the absolute values of frequency deviation, $\pm \Delta f$ Hz. The 'times threshold' values are less affected by training and by day to day variation in frequency discrimination than are the absolute values; mean values of the latter can be found by multiplying the $\pm \Delta f$ values of Fig. 2 by (\times Thr.) and some important mean absolute values are also specified in Table 1.

(b) Tuning of the conditioning effect in terms of modulation frequency

Considering first the measurements made at $f_0 = 250$ Hz, $\phi_{\text{test}} = 8/\text{sec}$ modulation frequency, a value in the middle of the middle 'regime' of frequency modulation detection illustrated in Fig. 2, we find that conditioning is maximal when $\phi_{\text{cond}} = \phi_{\text{test}} = 8/\text{sec}$ and that it results in a deterioration of detection sensitivity such that the frequency deviation in the test tone has to be increased to about three times the unconditioned values of detection threshold.

At conditioning modulation rates (ϕ_{cond}) removed from the test frequency of modulation (ϕ_{test}), the deterioration in detection sensitivity following exposure to the conditioning tone becomes much less marked when $\phi_{\text{cond}} = \frac{1}{2}\phi_{\text{test}}$ or $= 2\phi_{\text{test}}$ is almost absent. The raw data for this 'tuning' of the effect in terms of modulation frequency have already been published (Kay & Matthews, 1971) but are now shown here in Fig. 4 together with three, computer fitted and plotted, best fitting Gaussian curves for the three methods of testing, monaural, binaural and contra-aural.

It is evident (1) that the conditioning effect is tuned for modulation frequency and is maximal when $\phi_{\text{cond}} = \phi_{\text{test}}$, (2) that the magnitude of

the deterioration in detection sensitivity at the central modulation frequency of the tuning curve is by about 3 times for monaural conditioning and testing and is by about $2\frac{1}{2}$ times for the case of contra-aural conditioning, that is to say when the conditioning tone is fed to one ear and the following testing tone is then applied to the other ear, and (3) that the width of the curves is only a few c/sec in modulation frequency (see Table 1, later, for exact values) so that conditioning is almost absent when ϕ_{cond} lies outside 2/sec and 14/sec for monaural, or outside 5/sec and 12/sec modulation frequencies for contra-aural conditioning.

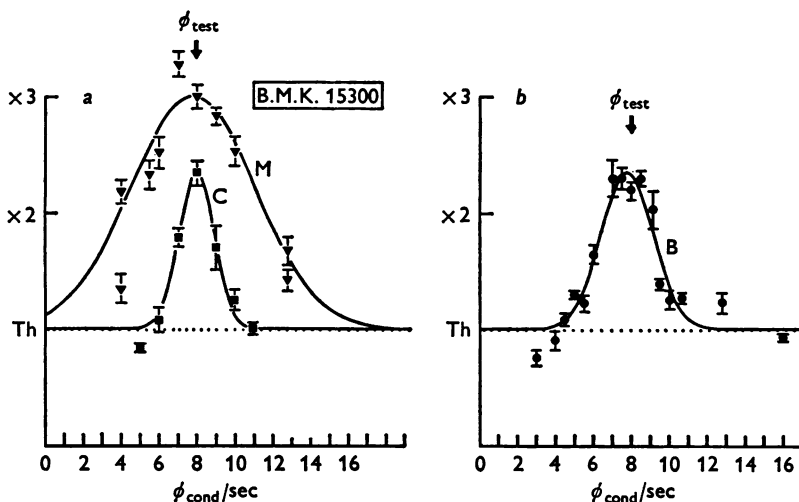


Fig. 4. The tuning of conditioning at modulation-frequency 8/sec. Ordinate: deterioration in detection sensitivity (\times threshold). Abscissa: conditioning modulation-frequency, ϕ_{cond} , per second. The test modulation-frequency, ϕ_{test} , is 8/sec throughout. The mean audiofrequency, f_0 , is 250 Hz throughout. M: monaural conditioning and testing (right and left ear results pooled). C: contra-aural conditioning and testing (condition-R/test-L results pooled with condition-L/test-R). B: binaural conditioning and testing.

That the effect transfers 'contra-aurally' from conditioning on one side to testing on the other to the extent of 80% the monaural conditioning strongly suggests that the major part of the effect is a central phenomenon.

Measurements like these were also made by conditioning and testing at modulation frequencies higher and lower than 8/sec and some curves corresponding to Fig. 4 are shown in Figs. 5a and b for these other modulating frequencies. We show in Fig. 6 all the binaural cases tested between $\phi_{\text{test}} = 0.25/\text{sec}$ and $= 120/\text{sec}$ plotted between common axes for direct comparison. The general conclusion is that conditioning exists for all

modulation frequencies between 1/sec and about 100/sec, that when it exists it is tuned with respect to modulation frequency and there is considerable interaural transfer of conditioning.

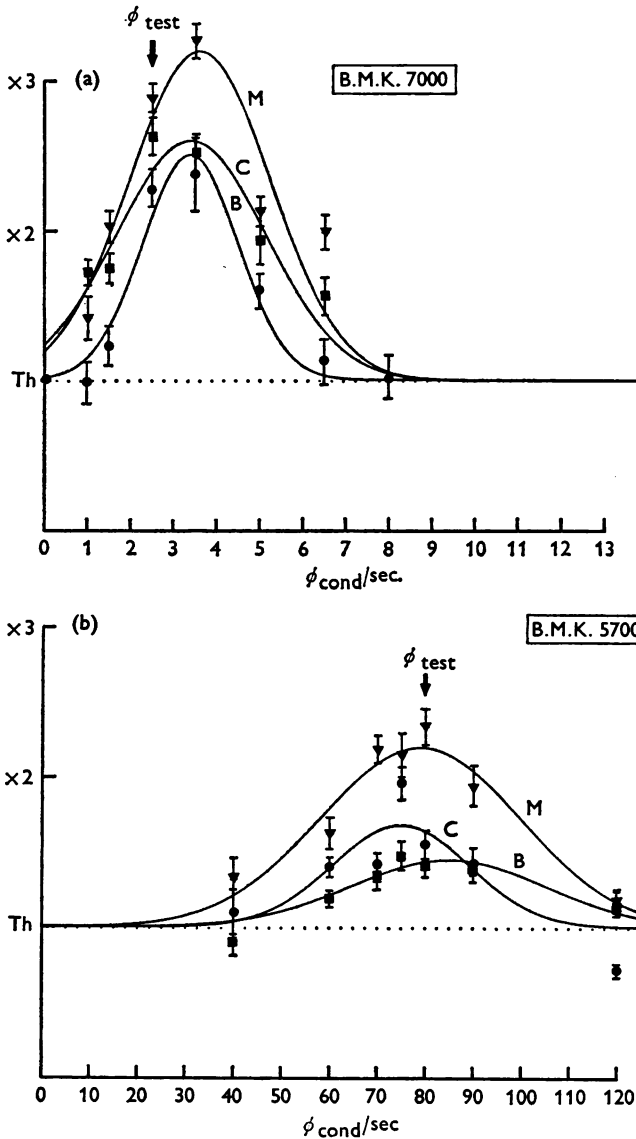


Fig. 5. The tuning of conditioning when testing at modulation frequencies, ϕ_{test} , (a) 2.5/sec (b) 80/sec. Ordinate: deterioration in detection sensitivity (\times threshold). Abscissa: conditioning frequency M: monaural. C: contra-aural. B: binaural. As in Fig. 4.

The main characteristics of the conditioning are summarized in Table 1, which, together with Fig. 6, shows that at lower modulation frequencies the peak of the tuned, conditioning effect (μ in Table 1) becomes more and more displaced towards a modulation rate *higher* than the test modulation frequency. It may be that these channels used to carry modulation become fewer and/or less effective for very low modulation rates and that this skews the tuning of the effect towards higher modulation frequency. In a

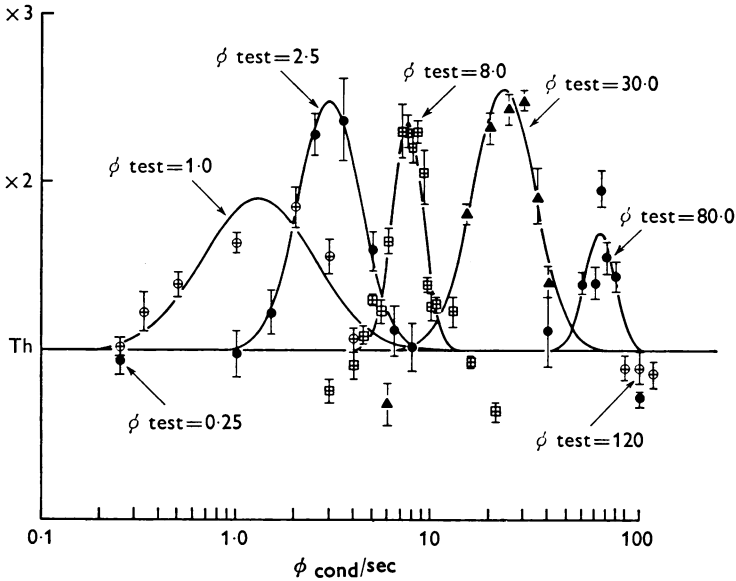


Fig. 6. The tuning of conditioning at modulation frequencies between 0.25/sec and 120/sec. Ordinate: deterioration in detection sensitivity (\times threshold) for named test modulation frequencies. Abscissa: conditioning modulation-frequency: logarithmic scale.

like way, the peak effectiveness of conditioning at high modulation frequencies becomes displaced towards a *lower* modulation rate than ϕ_{test} , possibly indicating a paucity and/or relative ineffectiveness of 'channels' capable of carrying the highest modulation rates for which the effect has been observed. This may also account for the smaller deterioration of detectability after condition (Y_0 , Table 1) at the lower and higher modulation rates. At intermediate modulation rates the peak conditioning rate, ϕ_{cond} , is centred on ϕ_{test} .

(c) *The dependence of conditioning on mean 'carrier' audiofrequency*

The above experiments were repeated but with modulation rate of frequency-modulated conditioning tone (ϕ_{cond}) kept identical with that

used for the test modulation (ϕ_{test}) but now at a variety of mean 'carrier' audiofrequencies ($f_{0 \text{ cond}}$) for the conditioning tones while keeping the mean test audiofrequency ($f_{0 \text{ test}}$) constant.

The conditioning effect is found to be maximal when $f_{0 \text{ cond}} = f_{0 \text{ test}}$ but the dependence of conditioning on mean audiofrequency, unlike the modulation frequency's effect, is poorly tuned in absolute terms and is at least ± 100 Hz wide for half effectiveness. The σ (see Table 1) for this tuning is 95 Hz whereas in terms of modulation frequency it is 1.4 c/s. For example, the sensitivity of detecting 8/sec frequency modulation in a test tone of

TABLE 1

ϕ_{test}	Y_0	μ	σ
0.25/sec	B 0.9 ⁵	—	—
1/sec	B 1.9	2.0	1.0
2.5/sec	B 2.5	3.4	1.1
	C 2.6	3.4	1.7
	M 3.2	3.6	1.6
8/sec	B 2.3 ⁵	7.8	1.4
	C 2.3 ⁵	8.0	0.9
	M 3.0	7.8	3.3
30/sec	B 2.5 ⁵	25.5	9.2
80/sec	B 1.7	75	14.3
	C 1.4 ⁵	85	20.5
	M 2.2	79	21.0
120/sec	B 0.9	—	—

B: binaural conditioning and testing.

C: contra-aural conditioning and testing.

M: monaural conditioning and testing.

Y_0 : deterioration in detection sensitivity (\times threshold) at the maximum of the 'tuning'.

μ : the value of ϕ_{cond} corresponding to Y_0 .

σ : the half-width, in c/sec of the Gaussian 'tuning' curves at 0.607 ($Y_0 - 1$).

mean audiofrequency 250 Hz is still significantly deteriorated by conditioning with tones also frequency modulated at a rate 8/sec but with the mean audiofrequency as low at 150 Hz or as high as 350 Hz (Fig. 7). This poor tuning is comparable in its magnitude with the width of 'critical bands' and like them may possibly be a peripheral phenomenon of the cochlear organization. Whatever 'channels' are uncovered by these conditioning techniques they are more concerned with specifying the frequency modulation wave than with the mean carrier audiofrequency.

*Independence of detection sensitivity to frequency modulation
from conditioning by amplitude-modulated waves*

We have tried to determine what aspects of the conditioning tones used in the experiments described above were adequate stimulus for conditioning and what were irrelevant, by measuring frequency-modulated detection thresholds after conditioning by either amplitude modulated or by frequency modulated waves and also by measuring the conditioning of amplitude-modulated detection thresholds after exposure to either frequency- or amplitude-modulated tones.

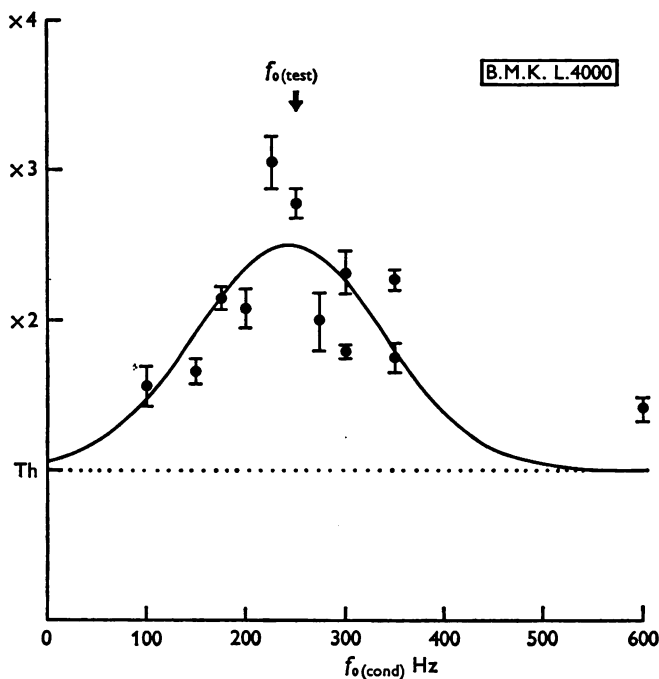


Fig. 7. Conditioning as a function of carrier frequency of the conditioning tone. Ordinate: deterioration in detection sensitivity (\times threshold) of a test modulation $\phi_{\text{test}} = 8/\text{sec}$ of carrier-frequency, f_0 , 250 Hz. Abscissa: conditioning carrier-frequency ($f_{0 \text{ cond}}$), the conditioning modulation-frequency being 8/sec throughout. Miss Lim Irene Kay Han acted as a fourth subject here.

Amplitude- and frequency-modulated tones are used for this comparison because, provided that the modulation rate is the same in each case, they share a common periodicity and also the time integrated spectra of the threshold detectable modulated test tones have like side bands, identically separated from the carrier frequency band (at threshold detectable depths

of modulation only the first side bands of the frequency-modulated test tones are of significant amplitude and sinusoidally modulated amplitude-modulated tones have in any case only the first side bands present; see Fig. 9). But amplitude and frequency modulation differ very much in terms of instantaneous parameters. The instantaneous frequency of a frequency-modulated tone changes and of an amplitude-modulated tone does not; the instantaneous amplitude of an amplitude modulated wave changes but of a frequency-modulated wave does not.

Some results are illustrated in Fig. 8. The frequency-modulated conditioning tones were as specified in the above experiments; the amplitude-

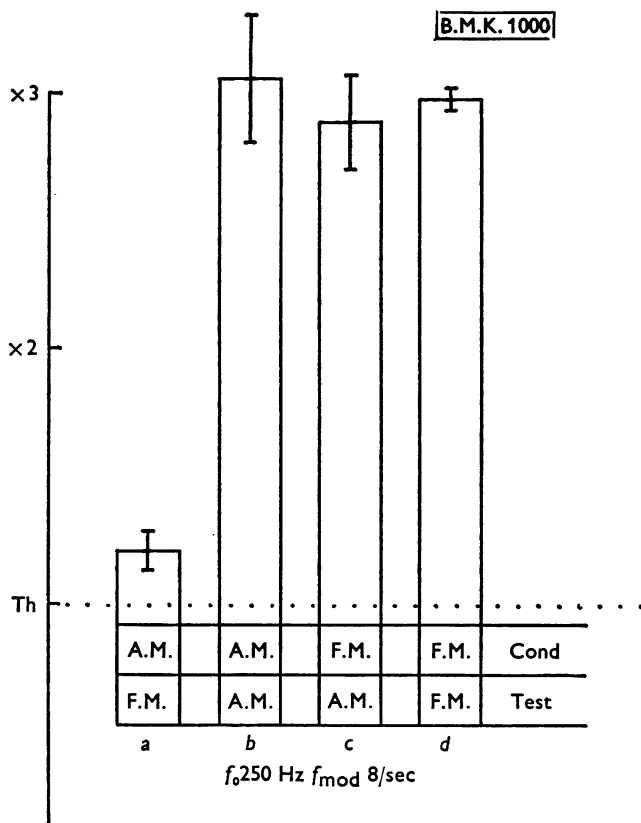


Fig. 8. Interactions between frequency-modulated and amplitude-modulated tones. Ordinate: deterioration in detection sensitivity (\times threshold) for modulation in a tone, $f_0 = 250 \text{ Hz}$, $\phi_{\text{test}} = \phi_{\text{cond}} = 8/\text{sec}$ when (a) amplitude modulation conditions frequency-modulation detection, (b) amplitude modulation conditions amplitude-modulation detection, (c) frequency modulation conditions amplitude-modulation detection, (d) frequency modulation conditions frequency-modulation detection.

modulated conditioning tones were 100% modulated, which maximally conditions amplitude-modulated detection sensitivity. Test and conditioning modulation frequencies were at 8/sec.

It is evident that there is a special response with respect to frequency-modulated detection sensitivity. Such conditioning tones affect the detection sensitivity to amplitude or to frequency modulation in a test signal. But although 100% amplitude modulated tones condition amplitude modulation detection, a 100% modulated amplitude-modulated tone leaves the detection sensitivity to frequency modulation in a test tone unaffected.

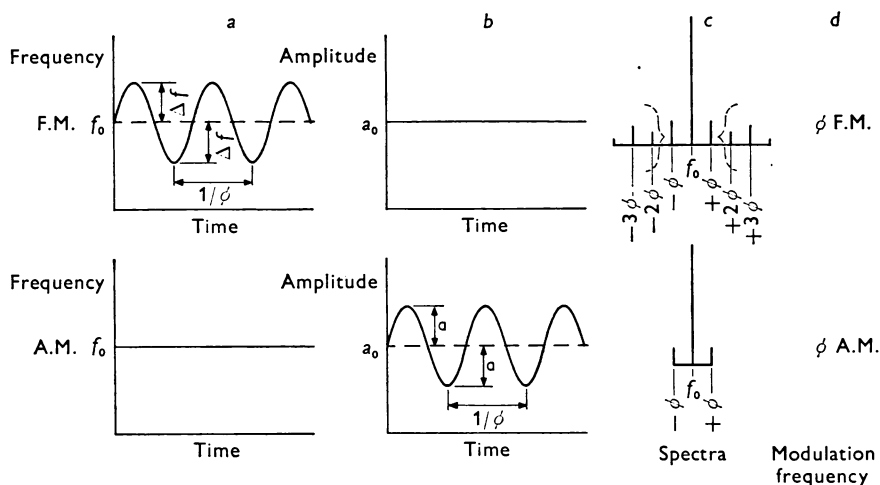


Fig. 9. Comparison of some characteristics of frequency-modulated and amplitude-modulated waves of the same carrier-frequency (f_0) and the same modulation frequency (ϕ). (a) Instantaneous frequency. Depth of modulation = $\pm \Delta f/f_0$. (b) Instantaneous amplitude. Depth of modulation = $\pm a/a_0$. (c) Time-integrated spectra. The upper diagram illustrates the general nature of any frequency-modulated (F.M.) spectrum, in which several side bands may be present and have amplitudes depending on modulation depth. The dashed brackets indicate that at the human threshold of detection for frequency modulation, only the first side bands $+\phi$ and $-\phi$ are present in the wave at significant amplitude. (d) Common modulation frequency. For some actual waveforms see Fig. 1.

This finding strongly suggests that the adequate stimulus for conditioning the detection of frequency modulation is a parameter unique to frequency modulation. This parameter is almost certainly the *instantaneous frequency variation* governed by the modulation waveform. The adequate stimulus is very unlikely to be any common characteristic shared by amplitude- and frequency-modulated tones, and not therefore mere periodicity of the modulation which is identical in the two cases, nor yet

coincidences in the positions of the (first) side bands in the conditioning and test tones, since at threshold detectability levels of modulation in the test tones only the first side bands are present to be conditioned. Their position and separation from the fundamental carrier band are identical in the amplitude- and frequency-modulated cases.

These experiments supplement and underline those in the last section on the poor dependence of frequency-modulated conditioning upon carrier frequency. Those experiments, by demonstrating, for example, that a conditioning frequency modulation centred at 150 or 350 Hz still conditions frequency-modulated detection at 250 Hz also demonstrate that coincident spectra cannot be the adequate stimulus, since spectra of these conditioning tones do not coincide with the spectrum of the test tone.

The conclusion is that these 'channels' which are conditioned by frequency modulation as described in this paper are little concerned with modulation periodicity *per se*, little concerned with signal spectrum, little concerned with mean 'carrier' audiofrequency but are much concerned with the instantaneous frequency changes carried in the modulation waveform of the frequency-modulated wave.

DISCUSSION

The essential conclusions from these experiments are summarized in the last paragraph of the results section above. What remains for more speculative discussion is (1) whether the sort of organization revealed is unique to the auditory pathways or is shared by some aspects of perception in other sensory modalities, (2) whether it is possible to suggest a neuronal model for the detection of frequency modulation and (3) whether a likely specific functional appropriateness can be seen in the organizational characteristics observed.

The most immediately tempting sensory pathway for comparison with the auditory is of course the visual. There is no doubt that Blakemore & Campbell's (1969) discovery of visual channels specifically concerned with spatial frequency of 'grating' light intensity patterns relies on exactly the same sort of technique used here and assumes that if a 'channel' can be fatigued in a man by an appropriate stimulus then it exists as a neural organization.

It is of course assumed that the physiological stimulus shall be physiologically undamaging and, if possible, even gentle; certainly not a sledge hammer. Thus Blakemore & Campbell were careful to keep the total luminance of their grating stimuli constant in conditioning and test stimuli, and of moderate and comfortable viewing levels, and also to insist on a wandering gaze so that after-images were not formed. Similarly, we

used throughout the comfortable listening levels around 40 dB which produce little after masking of intensity acuity, nor do we condition for times longer than the minimal necessary and thus we avoid fatigue. The fact that amplitude modulation does not condition frequency modulation is powerful evidence that we have succeeded in this respect. This effect is also testimony to the fact that the frequency-modulated conditioning effect is a 'physiological' one and not a 'psychological' one of e.g. perceptual criteria of frequency modulation *vs.* amplitude modulation because it is well documented, and we confirm, that subjects cannot distinguish frequency modulation from amplitude modulation in test tones at the threshold detectable modulation levels, yet these identical sounding tones have special treatment when the modulation is in fact frequency modulation; the 'sound' of the tone is thus not a clue, because the detection sensitivity to modulation in test tones that sound the same is conditioned differently.

Is there also, apart from technical procedure, any close physiological analogy between the visual channels found to be selective for spatial modulation frequencies of light intensity patterns and these channels selective for frequency modulation in sound? One complication in attempting a comparison is that whereas for visual stimuli time and space are separable as distinct characteristics of the optical stimulus to the retina, this cannot necessarily be assumed possible for the auditory system. In audition, apart from an intrinsic interdependence of time, frequency and spectrum in the stimulus itself, there is the added complication that space and frequency are interrelated at the peripheral receptive field. The peripheral stimulus is spread along the basilar membrane's carpet of mechanoreceptors with higher frequencies investing the basal regions of the cochlea, and lower frequencies the apical regions. This spatial correlation with frequency is preserved and even refined on the way up the tonotopically organized parts of the pathways. Thus, when there exists in audition an effectively 'spatial frequency' of a stimulus to the peripheral receptive field (e.g. a regular periodicity in the spatial pattern of activity in the pathways initially due to peripheral spatial peaks caused by spectral energy peaks in, say, a frequency-modulated tonal stimulus) it may be impossible, unlike in vision, to separate this 'spatial frequency' from the acoustically correlated temporal frequencies in the stimulus (e.g. in the stimulus already specified, the frequency of modulation generating the spectral peaks). It may therefore be unwise to push too far the evident analogies between the organization of the visual and auditory pathways that reveal themselves, because in vision *spatial* (Blakemore & Campbell, 1969) and *temporal* (Smith, 1971) aspects of the stimuli may be entirely separable, whereas in hearing they may not be. It would nevertheless be completely unrewarding entirely to ignore similarities of organization. It

may well be that Whitfield & Evans's (1965) cells in the cat sensitive to frequency-modulated tones are organized like Hubel & Wiesel's (1959) cells sensitive to moving visual stimuli. In a tonotopic and 'place' organization the analogue of a moving visual stimulus on the retina is a stimulus at the cochlea moving to and fro on the basilar membrane, i.e. one that is frequency modulated. Though Whitfield & Evans reported that modulation frequencies between 1 and 20/sec were effective in exciting frequency-modulated cells in the cat auditory cortex (a range not too unlike ours), they were not concerned at that time with discovering whether the frequency-modulated response is 'tuned' in modulation frequency. It would be interesting to know this, as a possible correlate with the human response. There are signs of tuning of this sort, in the sense of particular behaviour of selected parameters of a cell's discharge occurring in a restricted range of modulation frequency in Nelson *et al.* (1966) where their recordings in the cat inferior colliculus show what look like narrow 'half-widths' of modulation-frequency effects, e.g. their Fig. 11 *D-E* and Fig. 13 *A-F*. It may also be significant with respect to our conclusion concerning the special nature of man's frequency-modulated response that they report, in like sense, that although 'frequency-modulated tonal stimuli could elicit marked responses when amplitude modulation at the same centre frequencies did not; in only one case did an amplitude modulated stimulus elicit responses when frequency modulation at the same centre frequency failed to do so'.

How can these effects selective to frequency modulation arise? It is unlikely that integrated spectrum can have anything to do with the case for reasons already fully developed above. In addition, we should also notice here that we have been unable to detect in the 'tuning curve' of conditioning any subsidiary maxima when ϕ_{cond} is some submultiple of ϕ_{test} . For example, when $\phi_{\text{test}} = 8/\text{sec}$ there are no subsidiary maxima in the tuning curves at $\phi_{\text{cond}} = 4/\text{sec}$ or $= 2/\text{sec}$, yet at these conditioning frequencies side bands in the integrated spectrum of ϕ_{cond} coincide with spectral bands in ϕ_{test} . Furthermore, if the detection of frequency modulation by man has anything in common with the way in which a man *hears* frequency modulation then there is no doubt that what is perceived at most of the modulation frequencies described above, and certainly all those below about 10/sec, is indeed not side bands but 'instantaneous' frequency change such as might be displayed on a rapidly acting frequency meter (like Kay, 1965). It is at and above about 30/sec modulation rates that one begins to perceive the modulation as spectral bands 'colouring' the tone; it is also at modulation rates above 30/sec that these channels begin to peter out.

As to the function of these channels, it may be suggestive that the range

of frequency-modulation rates they cover, from very low frequencies to nearly 100/sec, is very like the range of modulation rates that the vocal apparatus normally makes. And, since the channels are relatively uninterested in carrier frequency, they may be the means whereby the significant message in an acoustic signal, e.g. the voice's frequency-modulation, is channelled independently of the relatively unimportant steady aspects of the signal like the mean carrier upon which the signal is impressed, i.e. the general pitch of the voice. It might be remembered here that speech loses little comprehensibility when it loses all its amplitude modulation (by 'peak clipping') but retains frequency modulation, whereas 'centre clipping', removing the zero-crossing frequency modulation is hopelessly damaging to the signal (Licklider & Miller, 1951). It may also be particularly significant that articulation scores are severely deteriorated when sound is switched to the ears at rates between 0.3/sec and 90/sec (Cherry & Taylor, 1954). It is just in this range of frequencies that our channels exist.

However this may be, it is clear that the channels are tuned for modulation of frequency, that judged by the high interaural transfer their arrangement must be predominantly in the central nervous system, that they are specially concerned with the modulation waveform of the frequency change, since signal spectrum and periodicity (which are similar in amplitude modulation) are not adequate stimuli for revealing the channels, and that they are relatively unconcerned with mean carrier frequency. There are already experiments from animal neurophysiology on cells especially concerned with frequency modulation. We hope that the channels rather fully defined here may help to suggest stimuli appropriate for a further neurophysiological attack on the location and coding responsible for this organization revealed in man.

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